INTEGRATING LICHEN
ENHANCEMENT WITH
PROGRAMS FOR
WINTER RANGE CREATION

PART 1: STAND/LICHEN MODEL

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

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INTEGRATING LICHEN ENHANCEMENT WITH PROGRAMS FOR WINTER RANGE CREATION

PART 1: STAND/LICHEN MODEL

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by

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ABSTRACT

The management activities necessary to enhance arboreal lichen abundance in second-growth stands are formulated into a strategy compatible with other aspects of winter range creation. The conditions that promote lichen colonization, lichen growth, and litterfall production are described. A set of key stand features that are indicators of the potential of a stand to produce lichen forage are identified. A computer model is used to relate stand development to the production of lichens and litterfall, and to predict the effects of several different management scenarios on the key stand features.

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1 INTRODUCTION

Abundance of arboreal lichens of the genera *Alectoria* and *Bryoria* is a key feature of winter range for black-tailed deer (*Odocoileus hemionus columbianus*). When heavy and frequent snowfalls cover much of the rooted forage, lichen litterfall may be a critical source of energy for deer (Nyberg *et al.* 1986). The availability of lichen litterfall to deer depends on three factors: the lichen biomass present in the canopy; the rate at which lichens are deposited on the forest floor; and the rate at which fallen lichens are covered by snow.

Optimum conditions for producing lichen litterfall as deer forage are ordinarily met in old-growth rather than in second-growth stands. However, demand for second-growth stands that can function as winter ranges for deer has led managers and researchers to ask whether availability of arboreal lichen litterfall in young stands can be enhanced.

Lichen biomass in canopies of second-growth stands is thought to be restricted primarily by the limited dispersal range of the major forage genera, and by the latter's preference for a microclimate that is relatively light, moist and cool, with frequent wetting/drying cycles (Stevenson 1985). The dispersal problem has been approached in two ways, each of which may be appropriate under some conditions. One is that patches of old-growth timber or lichen-bearing residuals may be retained as natural sources of lichen propagules for second-growth winter ranges (Stevenson 1988). The other way is that young stands may be inoculated with lichen fragments (Palmer 1986, 1987b). The problem of the unsuitable microclimate of young stands may be solved by a thinning program.

Concern has been expressed that litterfall rates in second growth may not be adequate to ensure that canopy lichens become available to deer (Nyberg *et al.* 1986). A recent problem analysis concluded that ordinary thinning would reduce litterfall rates substantially, but thinning methods that left standing dead trees would probably enhance lichen abundance while maintaining woody material as a source of lichens and litterfall (Stevenson 1986). Because snow covers litterfall and increases energetic costs for deer, prescriptions should also be designed to enhance snow interception.

Models for managing young stands to enhance cover and create understory forage have been developed (Nyberg *et al.* 1986). Phase 2 of the Integrated Wildlife Intensive Forestry Research Program (IWIFR) calls for experimental and operational creation of winter ranges for deer in young second growth. However, management activities necessary for lichen enhancement have not been formulated into a cohesive strategy compatible with other aspects of winter range creation. The purpose of this report is to develop a model for managing young stands to enhance lichen forage. The model is envisioned as a first approximation to guide research, and will in turn be modified by research results.

1.1 Objectives

The objectives of the project were:

1. to produce a conceptual model of stand development, indicating the effects that management actions are expected to have on lichen development and litterfall potential; and to suggest one or more scenarios for creating stands that will produce lichen forage and also meet other criteria for winter range;
2. to document research needs identified using the model, and to make plans to meet those needs; and
3. to prepare a plan to incorporate management for lichen production into experimental and/or operational winter range creation activities to be carried out by IWIFR.

Objective 1 is addressed in Part 1 of this report. Objectives 2 and 3 are addressed in Part 2 (Stevenson and Palmer 1988), a set of working plans on file with MacMillan Bloedel Ltd., and the B.C. Ministry of Forests, Vancouver Forest Region.

1.2 Methods

The conceptual model of stand/lichen development presented here is based on the literature on stand development, stand microclimate, and arboreal lichen ecology. We also relied heavily on the stand development model TASS (Mitchell 1975, 1980), developed by K. Mitchell and his associates at the B.C. Ministry of Forests (Forest Science Research Branch). We used a series of TASS runs to explore effects of various sets of management actions on variables expected to be related to production of lichen forage.

We also consulted researchers, managers, and others to help us develop working plans. The winter range creation plans were developed in consultation with IWIFR personnel.

2 STAND/LICHEN DEVELOPMENT MODEL

The potential of arboreal lichens to colonize a forest, grow, and become available to deer as litterfall depends on features of the stand that change during succession. In Section 2.1, we identify the conditions that are necessary for lichen colonization, growth, and litterfall production to occur. In Section 2.2, we identify key stand features which indicate a stand's potential to produce lichen forage, and discuss the production of lichen and litterfall as unmanaged stands develop. We then describe how those key stand features are affected by forestry practices (Section 2.3). Last, we present our model of stand/lichen development, which is the basis for management scenarios to enhance the production of lichen forage in second growth (Section 3).

2.1 Conditions for Development of Lichen Forage

The following discussion of dispersal, substrate, microclimate, and lichen growth rates is based primarily on an earlier review by Stevenson (1985) of published and unpublished information, updated where possible. The discussion of litterfall is based on a literature review by Stevenson (1986).

2.1.1 Source of propagules

Establishment of lichens in a young forest begins with the liberation of viable propagules from the parent plants and their transportation into the young stand.

In the genera *Alectoria* and *Bryoria*, the propagules that colonize young stands most rapidly are detached thallus fragments. Some species also produce ascospores (sexual propagules of the fungal component of the lichen) or soredia (vegetative propagules incorporating the fungal-algal symbiosis), both much smaller than thallus fragments. Stevenson (1988) found that colonization of 2-year-old Douglas-fir twigs was overwhelmingly dominated by thallus fragments; if spores or soredia were present on young twigs, they had not yet developed into recognizable thalli. Spores or soredia may have a role in lichen development over longer time periods or greater distances, but thallus fragments are the propagules that are most important in early colonization of second growth.

Thallus fragments are liberated from their parent plants and transported to new locations primarily by wind. Susceptibility of a lichen species to breakage and transport by wind depends on its morphology, and on its position in the tree canopy. On Vancouver Island, the proportion of *Bryoria* spp. to *Alectoria sarmentosa* is higher in second growth than in old growth. The fine-bodied morphology of most *Bryoria* species may make them more susceptible to breakage than *Alectoria sarmentosa*. Their characteristic location in the upper canopy exposes them to high windspeeds and gives thallus fragments a release height well above the ground (Stevenson 1988).

The effective dispersal distance of thallus fragments from a mature timber source is only partially understood. Stevenson (1988) reported that numbers of lichen fragments in second growth decreased to about 50% of their maximum values within about 100 m of their source, dropped to 10–15% of maximum at 300–400 m, and were consistently less than 5% of maximum beyond 450 m. The amount of lichen

present in mature timber is critically important to lichen establishment in adjacent second growth: lichen abundance was uniformly low in second-growth plots adjacent to mature timber supporting medium or low lichen levels.

Establishment of lichen fragments in second growth is also influenced by the amount of mature timber within dispersal range. The minimum size of mature timber blocks that are effective as propagule sources is not known. Air movements between mature timber and second-growth plots were not treated in that study and were probably a major source of unexplained variation in the data. Stevenson (1988) recommended that reliance on natural dispersal as a source of propagules for establishment of abundant *Alectoria* and *Bryoria* spp. should be restricted to second-growth stands within 350 m on the leeward side of mature timber supporting above-average lichen loads.

Alternatives to mature timber stands as sources of lichen propagules in second growth are lichen-bearing veterans and snags, and artificially applied inoculum composed of fragmented lichens. The effectiveness of retaining lichen-bearing residuals during harvesting needs evaluation. A pilot study on lichen inoculation has been conducted (Palmer 1986, 1987a), and working plans for further investigations are included in Part 2 of this report.

2.1.2 Substrate

For *Alectoria* and *Bryoria* to become established in a young forest, thallus fragments must be deposited on a suitable substrate, and must then become attached to it. Two principal modes of attachment occur (Stevenson 1985). First, thallus fragments coil and uncoil as they are alternately wetted and dried, and can become entangled among twigs and needles. Second, thallus fragments can become attached directly to the substrate by means of fungal hyphae; these structures are termed "holdfasts" or "hapters." Entanglement can occur within days or weeks; hapter formation can occur within a year (Stevenson 1985; Palmer 1987a). To aid the establishment of artificially applied thallus fragments, gelatin adhesive spray has been used (Palmer 1986).

Not all thallus fragments deposited on suitable substrates become established. Palmer (1986) reported that 7.75% of the counts of lichen thalli occurring naturally on 600 two-year-old twigs changed over a 1-month period. Immigration and emigration are constant processes on young twigs, as they are on older substrates.

For arboreal species of *Alectoria* and *Bryoria*, the most common substrate is bark of coniferous trees. Age-related changes in the moisture-holding capacity or chemistry of the bark of host trees do not appear to affect lichen abundance (Stevenson 1985). However, both colonization and retention of lichens are affected by bark texture, which typically changes from smooth and stable on young surfaces, to rough and unstable on older surfaces.

Rough bark surfaces favour colonization by fruticose lichens (Degelius 1964; Kalgutkar and Bird 1969). On young twigs, roughened areas of periderm, such as bud scale scars and injuries, offer good attachment sites (Palmer 1986). In young second growth, lichens are less common on long twigs than short twigs, despite their greater surface area. We suggest two explanations for this. First, longer twigs tend to have smooth, slippery bark, offering few attachment sites. Second, twigs that have grown rapidly tend to have widely separated needles, offering fewer opportunities for entanglement of thallus fragments. Palmer (1986) showed that 2-year-old twigs with few needles retained fewer lichen fragments than twigs with normal foliar development. Young twigs that have grown at an average or below-average rate — provided they have not experienced needle loss — appear to offer better opportunities for lichen establishment than do young twigs that have grown rapidly.

We have few data indicating how rapidly bark texture changes. A small sample of 10- to 15-year-old Douglas-fir trees indicated that nodules, which usually form before fissures, were typically present on portions of lower branches aged 8 years or more, but fissures were not (K. Palmer, unpubl. data, 1987). In contrast, on trees aged approximately 25–30 years, portions of branches 8 or more years old typically bore both nodules and fissures. Observed differences in bark maturation may have been related to

differences in tree age, growth rate, or site characteristics. Light intensity has an influence on early periderm formation in *Pinus resinosa* (Borger and Kozlowski 1972); bark ontogeny in Douglas-fir may be similarly influenced by high light intensity. Our limited observations suggest that lichen development may be limited by bark smoothness, particularly in very young (≤ 8 years) portions of the crown.

Bark instability can be another factor limiting abundance of arboreal lichens. The rate of exfoliation is greatest on rapidly growing trees and on trunks with long unbranched sections (Barkman 1958). Exposure influences timing of mature periderm formation in various conifer species (deZeeuw 1941). Yarranton (1972) observed scaling below the live crown of black spruce, but little scaling within the crown itself, and speculated that exfoliation reduced lichen abundance on older parts of the tree. Stone (1986) observed that *Usnea* spp., which were attached to the branch by a single holdfast, were more affected by bark scaling than were foliose species. Foliose species more often had lobes which remained on the bark adjacent to the peeled area.

It seems likely that *Alectoria* and *Bryoria*, which readily develop hapters and become entangled among twigs and needles, would have a low susceptibility to removal by bark scaling. Instability of the bark is more likely to limit the abundance of *Alectoria* and *Bryoria* on exposed trunk locations than in the crown.

2.1.3 Microclimate

To understand the physiological responses of a lichen species to variations in microclimate we need measurements of its seasonal photosynthetic and respiratory responses to light, temperature and thallus hydration. Those data do not exist for arboreal species of *Alectoria* and *Bryoria*. However, we can make some inferences about the microclimatic preferences of a species, based on its occurrence in nature.

In mature Vancouver Island forests of average density, *Alectoria* and *Bryoria* grow most abundantly in upper portions of the canopy. In more open, exposed forests they extend to the lower canopy. They are sparse at low elevations, although they may be locally abundant near lakes. Stevenson (1978) found that in the Nimpkish Valley, *Alectoria* and *Bryoria* were most abundant on moderate to steep south-facing slopes at elevations above 500 m, where tree growth was poor. The optimum environment for those genera on Vancouver Island appears to be one having high radiation, high input of moisture, high evaporation rates and, therefore, frequent cycles of wetting and drying (Stevenson 1985).

It is unclear whether decreased abundance of *Alectoria* and *Bryoria* at low elevations is more closely tied to moisture or temperature limitations. However, both types of limitations have implications for management of second-growth winter ranges. Because young second-growth stands are likely to be warmer and drier than old growth, those limitations are more likely to affect lichens in young stands. Stevenson (1988) presented data suggesting that in the warmer subzones of Vancouver Island, microclimatic conditions in young stands on exposed south-facing slopes were suboptimum for *Alectoria* and *Bryoria*, even though lichen development was good in the more moderate climate of the mature timber. Palmer (1987a) found that retention of inoculated lichen fragments was poorest in the portion of her study area having highest summer temperatures, although other factors may also have been involved. Spacing of young stands will maintain warmer, drier canopy conditions for longer periods of time. We believe that the limits of tolerance of *Alectoria* and *Bryoria* to low moisture and high temperature should be defined.

Within a lichen species, there may be ecotypes that are adapted to specific sets of environmental conditions. Those ecotypes may or may not display distinctive morphological characteristics. On Vancouver Island, three ecotypes of *Alectoria sarmentosa* have been tentatively identified by K. Kershaw (pers. comm., 1986): low- and high-light populations from mid-elevation sites, and high-light populations from high-elevation sites. Understanding ecotypic variation may be essential to management. For example, it may be important to select for inoculation lichens that are suited to the microclimatic environment of the target stand (Palmer 1987a; K. Kershaw, pers. comm., 1986).

2.1.4 Time

Lichens need time to develop from small thallus fragments to clumps that are large enough to be useful as forage. Stevenson (1985) reported two indirect estimates of annual growth rates of *Alectoria* and *Bryoria*: 5–14% (mean = 8.5%), based on biomass of lichens on aged branches (K. Simpson, unpubl. data, 1983), and 10.5–16.1% (mean = 12.4%), based on litterfall rates as a percent of standing crop in an old-growth stand assumed to be at equilibrium (Stevenson 1978). Stone (1986) has measured the growth of whole thalli of the arboreal fruticose lichen *Usnea subfloridana* under field conditions, and calculated an annual growth rate of 29.4%.

New growth can often be identified on lichen fragments that have been broken, grazed, or cut. Three *Bryoria thalli* on branches inoculated by Palmer (1986) exhibited relative linear growth rates of 9.5%, 14.9%, and 28.6% (mean = 17.7%) when measured 1 year later (K. Palmer, unpubl. data). Palmer (1987a) considered those growth rates to be below the potential of the lichens because of the energy they presumably expended in establishing themselves in new surroundings.

Figure 1 shows the hypothetical time required for lichen biomass to reach mature forest winter range levels at several possible annual growth rates, as measured by Stevenson (1978). In the absence of any data on total lichen biomass in young Douglas-fir stands, the value of 1 kg/ha was chosen as an arbitrary starting point. The figure is not a realistic representation of lichen development in a stand, because it does not account for subsequent additions or losses of lichen biomass. Lichens arriving after Year 0 would cause the biomass curve to rise more rapidly in early years. As lichen biomass accumulates, litterfall rates increase, causing the curve to level off. The figure suggests that the time required to achieve high levels of arboreal lichen biomass is sensitive to small differences in two variables: annual growth rate and initial lichen biomass.

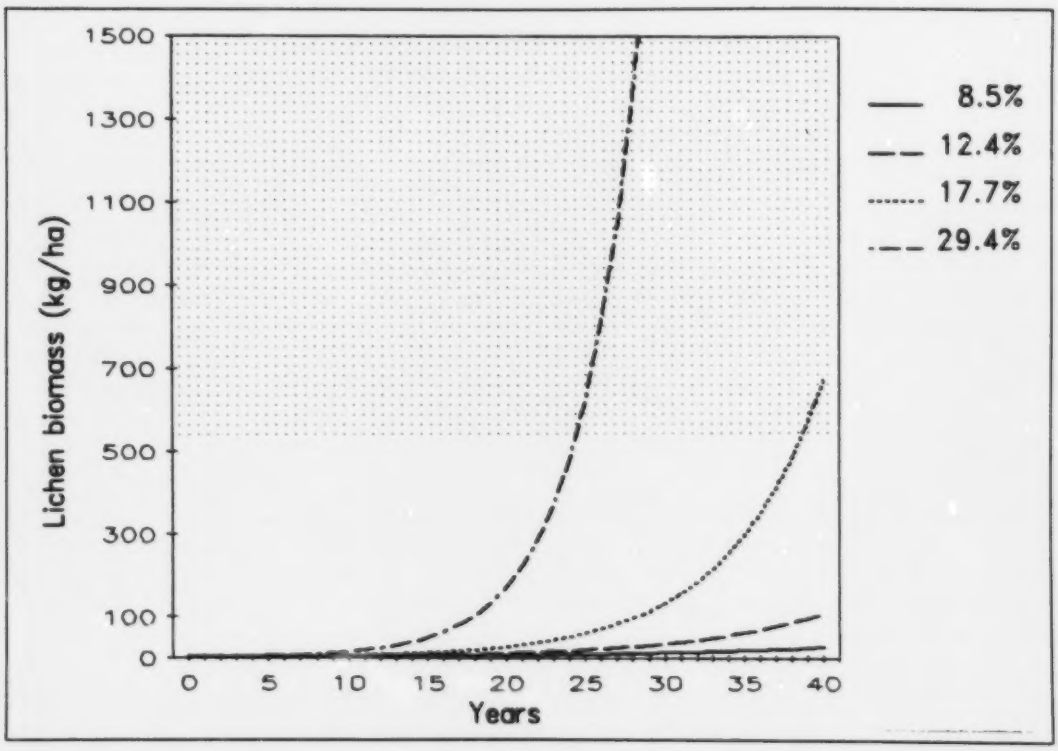

FIGURE 1. Hypothetical time required for lichen biomass to reach winter range values (stippled area) at several possible annual growth rates.

2.1.5 Litterfall

The amount of arboreal lichen available to deer over winter depends on lichen biomass in the canopy and the rate at which the lichens are deposited on the forest floor. Stevenson (1986) reviewed the literature on litterfall to assess the extent to which litterfall rates would limit availability of lichen forage in second-growth stands, assuming that their establishment and growth could be enhanced through special management techniques.

Lichens arrive on the forest floor either independently, or attached to branches, boles, or bark of trees. Litterfall rates of unattached lichen clumps are related to the standing crop of lichen in the canopy. Since large clumps of lichen are more likely than small clumps to break off and fall independently, litterfall rates may be proportional to the standing crop at high but not at low levels of the crop.

The amount of lichen that falls attached to woody parts of trees is probably related to the overall rate of woody litterfall in the stand, as well as to lichen standing crop. In a stand of Garry oak (*Quercus garryana*) aged about 120 years, 55% of arboreal lichens reaching the ground as litterfall were attached to twigs, branches, or bark, and 45% were loose (Pike 1971). Applicability of those results to stands of Douglas-fir or western hemlock is unknown.

Maximum reported rates of lichen litterfall are higher in mature stands than in immature stands. That difference probably occurs for two reasons. First, lichen standing crop is greater in older stands than in younger ones. Second, woody litterfall rates are higher in older stands than in younger ones, probably because of greater stand biomass and gradual death of trees from senescence. About one-third as much woody litter fell in young (20–100 years) Douglas-fir stands as in old-growth (>300 years) stands reviewed by Stevenson (1986).

Assuming that special management practices succeeded in producing as much lichen in second growth as in old growth, and that those practices did not affect litterfall rates, Stevenson (1986) estimated that 65 kg/ha of lichen litterfall per winter could be produced in second growth on a representative severe winter range site, and 106 kg/ha on a mild winter range site. If only 50% as much lichen were produced in second growth as in old growth, litterfall would drop to 37 and 53 kg/ha on the severe and mild winter range sites, respectively. Those amounts of lichen litterfall represent 32–64% of those observed in old growth, and would provide 25–73 deer days per hectare of forage on a severe winter range, and 36–120 deer days on a mild winter range.

The validity of the assumption that litterfall rates are unaffected by special management practices used to enhance lichen abundance depends on the practices. Effects of possible management practices on litterfall production are discussed in Section 2.3.

2.2 Stand Structure and Production of Lichen Forage

2.2.1 Key stand features for lichen production

In the following sections we evaluate changes in arboreal lichen habitat that occur during natural succession, as well as in response to forestry practices. To do that, we need to identify some measurable features of stands that are sensitive to changes in stand structure and that indicate suitability of a stand to produce arboreal lichens and lichen litterfall.

In this section we limit our discussion to sites which are microclimatically suitable for lichen production, as indicated by lichen abundance in old growth on comparable sites. We further assume that a source of lichen propagules for colonization is available, either naturally or through special management practices. Key stand features fall into three broad categories:

1. measures related to structure and biomass of the tree canopy;
2. measures related to tree growth; and
3. measures related to rate of woody litterfall.

Measures related to the canopy

The structure and biomass of the tree canopy are major determinants of the vertical profile of microclimatic variables within a forest stand. Evidence suggests that the optimum microclimate for abundant production of *Alectoria* and *Bryoria* on Vancouver Island has high radiation, high input of moisture, high evaporation rates, and, therefore, frequent cycles of wetting and drying (Section 2.1.3). It is likely that high temperature or low humidity can be limiting. To characterize the suitability of stands of various ages and management treatments for lichen production, we need to identify a set of stand measures that are related to the penetration of light and precipitation, and to the temperature and humidity in the canopy.

- **Foliage measures:** Because of the direct action of foliage on stand microclimate, foliage measures such as foliar biomass, total leaf area, and leaf area index (LAI) (an index of foliage area per unit of ground) should be related to all variables of interest. Average irradiance at any level in a canopy is related to irradiance above the canopy, an extinction coefficient, and leaf area index cumulated from the top of the canopy down (Jarvis *et al.* 1976). Throughfall precipitation is a function of storm size and canopy storage, which is about 0.2 LAI (Rutter 1975; cited in Bunnell *et al.* 1986). We are not aware of specifically documented relationships between foliage measures and stand temperature or humidity.

  The best predictions of vertical profiles of microclimatic variables in forest stands would likely be based on foliage measures such as leaf area index. However, following the reasoning of Bunnell *et al.* (1986), we have chosen an alternative approach. Our present needs are best met by simple, readily available measures of canopy openness. Foliage measures are rarely made directly in forest stands, but are estimated from allometric equations based on DBH relationships (Gholz *et al.* 1976; Waring *et al.* 1978). If stand attributes based on mensurational data or other easily obtained measures can be used as surrogates to LAI, then hypothesized relationships can be more easily tested.

- **Canopy cover:** Canopy cover and related measures have often been used as simplifying expressions of canopy density. We have adopted the definition of Bunnell *et al.* (1985) for canopy cover: the proportion of the ground surface encompassed by vertical projections of the outer edges of tree crowns. We reserve the term "crown closure" to refer to that time in stand development when the crowns of adjacent trees begin to meet and overlap. Mean crown completeness (*sensu* Bunnell *et al.* 1985) is a stand measure determined from a number of point measures of the proportion of the sky obliterated by tree crowns within a defined angle. It includes holes within, as well as between, tree crowns. Methods of quantifying mean crown completeness have been reviewed by Vales and Bunnell (1985).

  Various measures of mean crown completeness have often been related to light penetration. Figure 2 shows results of three studies that related mean crown completeness to global (direct and diffuse) solar radiation under the canopy (the curves are not extrapolated beyond the range of mean crown completeness values studied). Proportions of the variability accounted for by the regressions were high (86% or more). Mean crown completeness has also been related to interception of precipitation (Bunnell *et al.* 1986).

  Mean crown completeness has limitations as a predictor of penetration of light into the canopy. Alaback (1982) found that although mean crown completeness had a significant negative relationship with understory development in stands aged less than 100 years, it was uniformly high in older age classes and therefore a poor predictor of understory development. Stevenson (1978) also found that mean crown completeness was not useful in distinguishing among mature forest stands which appeared to vary in their light regime, perhaps because the regenerating tree layer was included in the measurements. Mean crown completeness is probably more useful in indicating gross changes in light regime in second-growth stands brought about by crown closure or thinning.

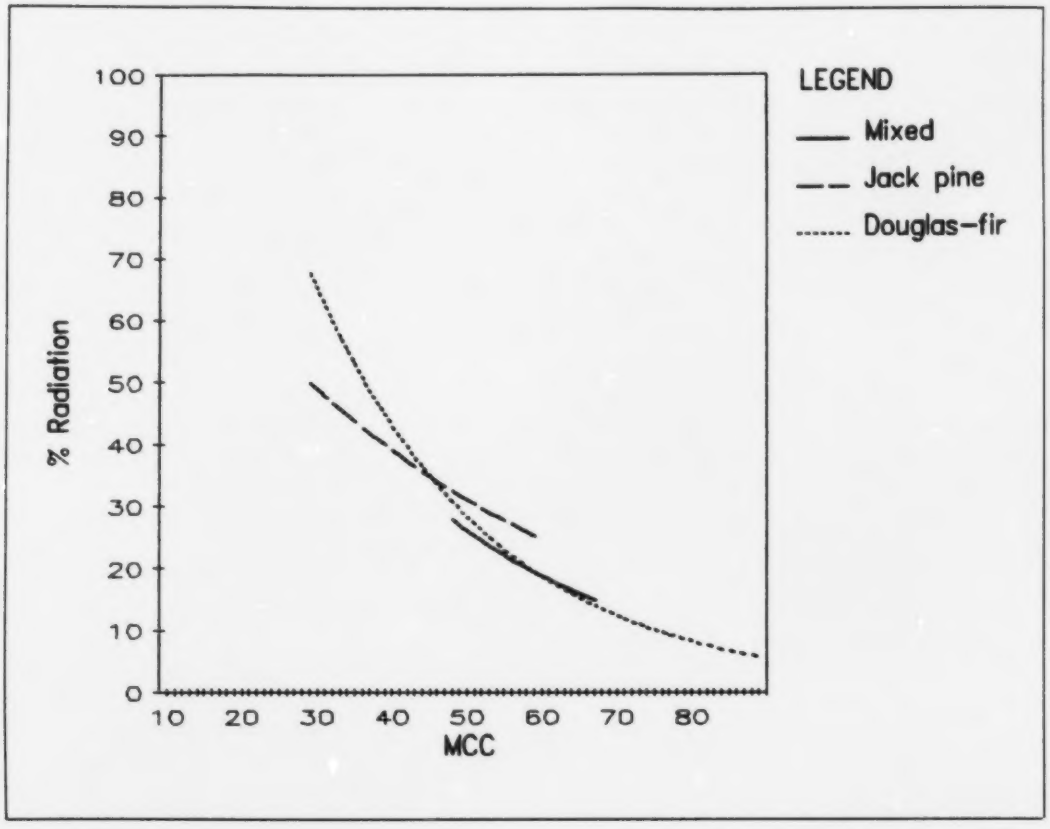

FIGURE 2. Effect of mean crown completeness (MCC) on global radiation under canopy as a proportion of radiation in the open. Equation for jackpine from Vézina and Péch (1964) (r^2 not given) as corrected by Bunnell *et al.* (1986); equation for mixed forest from Mayer (1981) (r^2 = 0.96); equation for Douglas-fir from Vales (1986) (r^2 = 0.86).

- **Crown depth:** If mean crown completeness alone determined light penetration, then % transmission and mean crown completeness would be expected to sum to 100. But that never occurs (Miller 1959, cited in Bunnell *et al.* 1986; Vézina and Péch 1964). The three-dimensional nature of the canopy, crown depth as well as closure, is believed to influence light penetration. Vales (1986), however, found that as a single variable crown depth did not predict transmission well, and that coefficients for crown depth in multiple regressions were not significantly different from zero.

  The relationship between crown depth and light penetration may be more complex than is immediately apparent. Deep crowns are expected to intercept more light than short crowns. However, deep crowns are most likely to develop in stands in which light transmission is high and dieback of lower branches is reduced. Thus, deep crowns intercept light but may themselves be indicators of high light penetration, whether because of low tree density, topography, or other reasons. That confounding may account for the inconclusive results of Vales (1986).

  The key variable affecting arboreal lichen habitat is not the amount of light transmitted to the forest floor, but the amount of light reaching suitable substrate in the canopy. Stevenson (1978) attempted to relate percent live crown, a measure of crown depth, to the abundance of *Alectoria* and *Bryoria* in mature forests in the Nimpkish Valley, Vancouver Island. She found percent live crown was positively correlated with lichen abundance, though the relation was weak. Lichen

abundance was consistently low in stands having low percent live crown, but was not necessarily high in stands with high percent live crown. Some variation may have occurred because the significance of percent live crown differs among tree species, and species composition varied among plots. In other cases, plots with high percent live crown but low lichen abundance were outside the range of site characteristics (elevation and topography) associated with high lichen production in that study area. High percent live crown may have some usefulness as an indicator of lichen habitat in mature forests, but it is difficult to interpret.

- **Stand measures:** Vales (1986) found that the sum of diameters of trees in his plots and Reineke's (1933) stand density index were good predictors of transmission of solar radiation to the forest floor on Vancouver Island salal sites. The sum of tree diameters was thought to have predictive value because it integrates leaf area (which can be predicted from tree diameters) and tree density (Vales 1986). The stand density index is the number of trees per hectare that would be observed if the quadratic mean diameter were 25 cm. It integrates tree size and basal area, and is expected to be a useful indicator of tree foliage and stand density (Vales 1986). It has been related to key events in stand development, such as onset of competition and self-thinning (Long 1985). Relationships between lichen abundance and stand measures such as sum of tree diameters and stand density index should be evaluated.

Tree growth measures

The growth rate of trees is thought to be negatively related to lichen abundance, although no relationship has been conclusively demonstrated. Stevenson (1978) showed a significant negative relationship between lichen abundance and height of the co-dominant tree layer in mature stands, but those results may be explained in several ways. There are two reasons for believing that slowly growing trees may offer better conditions for lichen growth than rapidly growing trees. First, young twigs that grow rapidly tend to have smooth bark and widely spaced needles, offering fewer attachment sites for lichen fragments than twigs that grew at average or below-average rates (Palmer 1986). Second, the microclimate in the canopy of a rapidly growing stand changes rapidly as branches become overtopped and shaded. A slowly growing stand offers a more stable microclimate for lichens than does a rapidly growing stand.

The growth rates of twigs in very young stands can be easily measured by the internode lengths on accessible branches. Such measurements may be useful to identify sites with a good potential for arboreal lichen development. For Douglas-fir, internode length decreases with increasing internode number from the bole (Long 1982); that is, twig growth rates decrease from the tip to the base of the crown. That pattern of branch extension results in considerable self-shading below the 11th whorl from the top (Long 1982). Although the exact relation would vary from one part of the crown to another, in general, branch growth rate should be related to annual height growth (S. Northway, pers. comm., 1987). Annual height growth should also be related to the rate of overtopping and self-shading of foliage.

Litterfall measures

Because of the apparent importance of woody litterfall in transporting arboreal lichens from the canopy to the forest floor, a measure of the rate of woody litterfall, or even of total litterfall, is desirable. Bray and Gorham (1964) cited studies correlating annual leaf litterfall with basal area in a series of evergreen and deciduous stands (Bonnevie-Svendsen and Gjems 1957) and total litterfall and basal area in *Pinus echinata* stands (Crosby 1961). Structural litter (bark, twigs and lichens) was significantly correlated with stand basal area in 15 *Pinus banksiana – Picea glauca* stands of various ages (Fyles *et al.* 1986). Reukema (1964) found that over a 13-year period, total litterfall was nearly proportional to basal area in a set of Douglas-fir stands repeatedly thinned to various prescriptions. These studies suggest that basal area may be a useful surrogate for total litterfall, when treatment effects are compared over time in successional Douglas-fir stands.

Basal area as an index to litterfall does not distinguish between effects of chainsaw thinning and thinning methods that leave standing dead trees, because generally only living stems are included in basal area determinations. When the effects of forestry practices on litterfall are compared, the contribution of snags must be considered. The rate of deterioration of snags varies with species, site characteristics, and snag diameter. Snags deteriorate more slowly on xeric sites than on wetter sites (Franklin 1986; J.P. Kimmins, pers. comm., 1986). Cline *et al.* (1980) described stages of deterioration of Douglas-fir snags and developed survival curves for snags of various diameter classes. Potentially useful measures related to the contribution of snags to woody litterfall might be number of hard snags (Stages 1 and 2 of Cline *et al.* 1980) per hectare, and basal area of snags. The latter measure has the advantage of being weighted in favour of larger snags, which make a greater contribution to litterfall over a longer time period than do smaller snags.

STAND FEATURES USED IN MANAGEMENT SCENARIOS

We identified a set of measurable stand features potentially useful as indicators of the suitability of a stand to produce lichen forage for deer.

Although foliage measures such as LAI are closely related to vertical profiles of microclimatic variables in forests — and thus to lichen habitat — they are rarely available. Various measures of canopy cover express canopy density more simply and have been related to penetration of light and precipitation. Because canopy cover is readily measured in the field and is a common output variable in stand development models, it was selected as an indicator variable for the management scenarios discussed in Section 3.

Crown depth and canopy cover are believed to influence vertical profiles of microclimate and lichen abundance in stands, but the relations appear to be complex. Percent live crown, a measure of crown depth, is included in the management scenarios in Section 3 because it contributes to an understanding of stand structure. However, no direct inferences may be made about its relations with lichen habitat.

Two stand measures, the sum of diameters of trees per unit area and Reineke's (1933) stand density index, have been related to transmission of light to the forest floor. Relations with lichen abundance have not been tested, but seem promising. The stand density index, which is easily derived from mensuration data or from output of a stand development model, is included in Section 3.

Tree growth rates are thought to be negatively related to lichen abundance, although more data are needed to test that hypothesis. Annual height growth is included as an indicator variable in the management scenarios.

Because of the apparent importance of woody litterfall in transporting arboreal lichens from the canopy to the forest floor, measures of litterfall rates are needed. Correlations between basal area and total litterfall have been demonstrated, and that variable is included in Section 3. To account for the contribution of snags created by thinning to litterfall rates, we have used snag survival curves to calculate the number of hard snags per hectare, and basal area of snags.

2.2.2 Succession in unmanaged stands

Developmental changes in stand structure result in changes in stand microclimate. Both structure and microclimate affect the suitability of a stand as lichen habitat, and the rate at which lichens are deposited on the forest floor. The following description of successional changes in structure and microclimate in an unmanaged Douglas-fir stand is adapted from Stevenson (1985). The general conceptual model of forest succession is based on Harcombe's (1984) recommendation that features from the schemes of Thomas (1979) and Walmsley *et al.* (1980) be combined. Figure 3 is based on output of the individual tree stand model TASS (Mitchell 1975, 1980) for Site Index 35. Variables are described in Section 2.2.1, and defined in Appendix 1.

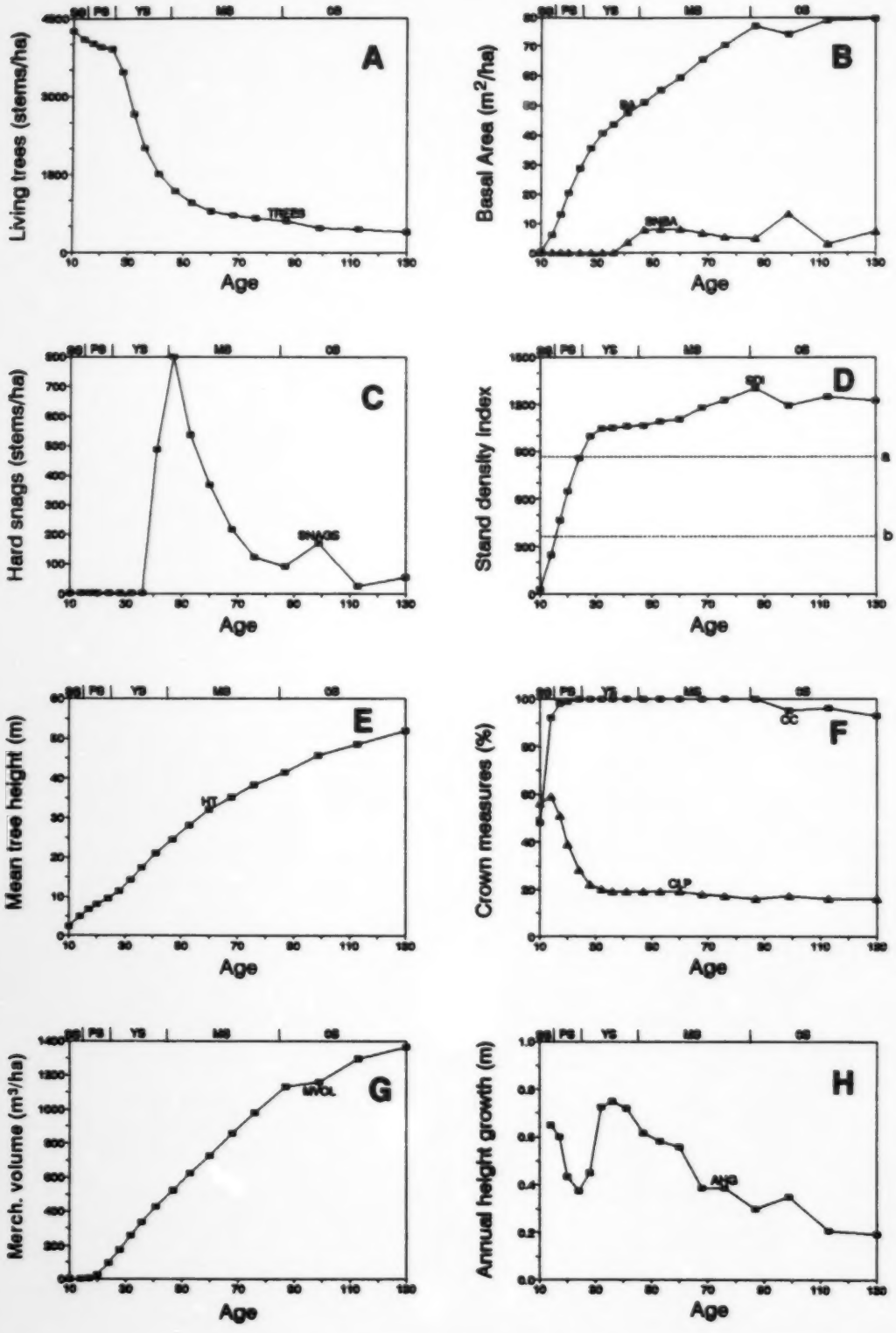

FIGURE 3. Successional changes in stand features in an unmanaged stand. A) TREES (stems/ha). B) BA and SNBA (m^2/ha). C) SNAGS (stems/ha). D) SDI: a = lower limit of self-thinning, b = onset of competition. E) HT (m). F) CC and CLP (%). G) MVOL (m^3/ha). H) AHG (m). Ss = shrub-seedling stage; ps = pole-sapling stage; ys = young seral stage; ms = maturing seral stage; os = overmature seral stage.

Grass-forb stage

During the grass-forb stage, tree seedlings are surrounded by a layer of broad-leaved vegetation, which on Vancouver Island is more often composed of herbs and shrubs than grasses. The broad-leaved vegetation affects both the development of trees and the microclimate of the site. Tree form is not yet affected by intraspecific competition. Brush competition, mainly for light, may result in changes to developmental features, such as an increase in specific leaf area (development of shade leaves) and a reduction in basal area growth in relation to height growth (Brand 1986).

The microclimate of an area during the grass-forb stage is more severe than that within a forest, but generally less severe than that over bare ground, because of the modifying influence of the vegetation (Geiger 1966). Solar radiation is high, maximum and minimum air temperatures are extreme, and humidity is low (Bell *et al.* 1974; Lee 1978). Wind speed is higher than it is under the shelter of a mature forest, though not as great as in the treetop zone, because of the general increase in wind speed with height above the ground (Geiger 1966). Because wind speed affects the movement of radiative heat, the microclimate near the ground during the grass-forb stage may be more severe than that of the treetop zone of a mature forest. Arboreal lichens are rarely present on seedlings.

Shrub-seedling stage

During the shrub-seedling stage, trees have grown above the broad-leaved vegetation, but the canopy has not yet closed. The crowns of young trees are exposed to light, and they still have an open-grown form. The microclimate is similar to that of the grass-forb stage, but is increasingly moderated by vegetation. If a dispersal source is present, lichen fragments colonize branches and stems on suitable sites. Exposed, low-elevation, south-facing slopes may be suboptimum (too warm or too dry) for *Alectoria* and *Bryoria* during this successional stage (Section 2.1.3).

Pole-sapling stage

Canopy closure occurs at the beginning of the pole-sapling stage (Figure 3F). Solar radiation below the level of canopy closure is much reduced. In a chronosequence of fir stands studied by Mitscherlich (1940, cited in Geiger 1966), light intensity at the forest floor dropped abruptly to about 10% of that in the open after the canopy closed. The lower portion of the canopy develops a microclimate similar to that of the shaded crown zone in older stands (Table 1). Although lichen development at the pole-sapling stage has not been studied, it seems likely that the microclimate that develops in the lower canopy is not suitable for *Bryoria* and *Alectoria* fragments that establish themselves during the shrub-seedling stage unless the stand is opened.

TABLE 1. Canopy position and microclimate in a coniferous forest (Stevenson 1985:13)[a]

Canopy position	Solar radiation	Temperature variation	Precipitation	Wind speed	Relative humidity	Evaporation
Treetop zone	H	H	H	H	L	H
Lighted crown zone	H–M	H–M	H–M	H–M	M–L	H–M
Shaded crown zone	L	L	L	L	M	L
Trunk zone	L	L	L	L–M	M	L–M
Tree base zone	L	L	L	VL	H	L

[a] H = high; M = moderate; L = low; VL = very low.

Lichen establishment continues in the lighted portion of the crown, but branches are quickly overtopped and shaded. Lower branches die. That process is reflected in Figure 3F as a rapid decrease in percent live crown during the pole-sapling stage. Woody litterfall, which up to now has been insignificant, increases as dead branches break off.

YOUNG SERAL STAGE

During the young seral stage, natural thinning begins. That is reflected in Figure 3 as a rapid drop in number of stems per hectare and a peak in the number of Class 1 and 2 (hard) snags. Following the classification of Cline *et al.* (1980), we define Class 1 as a deterioration stage in which most limbs and branches are present, and Class 2 as a stage of rapid branch loss, ending when all fine branches and most limbs are absent. Snags produced during the early seral stages are mostly small (< 19 cm DBH). If the patterns of deterioration observed by Cline *et al.* (1980) in western Oregon apply to Vancouver Island, snags probably lose most of their limbs during the first 8 years after death. Woody litterfall is composed mainly of deteriorating snags and lower branches of living trees, which continue to die back.

During the young seral stage, the vertical differentiation of microclimatic zones is that shown in Table 1. Lichen abundance is typically very low, but is moderate in some exposed, south-facing stands. If significant amounts of lichen are present, the greatest abundance seems to be primarily in the lighted crown zone and secondarily in dead or dying branches of the trunk zone. That bimodal distribution pattern may be related to light penetration, evaporation rates, or both. If lichens are present in significant amounts, they are probably also represented in the litterfall.

MATURING SERAL STAGE

In a maturing seral stand, the rate of natural thinning declines and stabilizes (Figure 3A). New snags are fewer in number but larger than they were during the young seral stage; loss of limbs is projected to occur over a 13-year period (Cline *et al.* 1980). Natural thinning increases the light levels reaching the forest floor and the main canopy. The whipping action of windblown branches also contributes to development of spaces among crowns of tall trees (K. Mitchell, pers. comm., 1987). A regeneration layer may become established, affecting the microclimate in the lower part of the stand by intercepting radiation and precipitation, increasing humidity, and lowering wind speed and evaporation. In slowly growing stands, lichen development may approach the potential of the site by the end of the maturing seral stage.

OVERMATURE SERAL AND MATURE CLIMAX STAGES

During the overmature seral and mature climax stages, tree growth slows and most stand characteristics are stable (Figure 3). The apparent increase in number of snags at age 99 is an artifact of the model. It is reflected in other measures, such as merchantable volume and basal area, and also appears in some treatment scenarios. It occurs because the regimes for mortality due to overtopping and to senescence are not well enough meshed (K. Mitchell, pers. comm., 1987). During these stages, individual trees in the main canopy that die are replaced by regeneration. The canopy is somewhat more open than before, reflected in Figure 3F by a slight decrease in crown closure. The characteristic microclimatic profile of a mature stand is summarized in Table 1, and was described in more detail by Stevenson (1985).

2.3 Effects of Management Practices on Forage Lichen Production

The developmental pattern described in Section 2.2.2 may be altered dramatically by some of the management practices that have been proposed for use in winter range creation.

2.3.1 Retention of lichen-bearing trees

Retention of lichen-bearing trees during harvesting and thinning has been proposed as a method for ensuring lichen propagules are available to colonize the regenerating stand. The necessary number and distribution of veterans have not been studied. Nyberg *et al.* (1986) recommended retention of at least two

veterans per hectare where winters are moderate, and at least four per hectare where winters are severe. Trees that are to remain standing for the longest possible time should be selected for this purpose. They should be living and windfirm.

Retention of small numbers of veterans is unlikely to affect other winter range values, but there are costs associated with that practice. Timber volume of retained veterans will be foregone if they are no longer merchantable at the next harvest. To minimize losses, low-value trees may be selected for retention, but the risk of restocking the site with poor genetic material would be increased. Finally, harvesting, site preparation, and stand tending procedures are more difficult when a few trees must be protected.

2.3.2 Choice of tree species for regeneration

Choice of tree species for regeneration may affect the potential of a site to support lichens. Of the three tree species that dominate winter ranges, mature Douglas-fir and western hemlock appear to be about equal in ability to support abundant lichens, although twigs of young Douglas-fir retain lichen fragments better than do twigs of young hemlocks (S. Stevenson, unpubl. data, 1977, 1978). In contrast, western redcedar supports conspicuously lower lichen loads. Managing for an overstory of Douglas-fir or western hemlock is consistent with both winter range values and forestry objectives.

2.3.3 Thinning

Effects of thinning on stand structure

Thinning a young forest stand is a standard silvicultural technique that increases diameter and volume growth of individual trees. It also results in important changes in canopy structure (Brix 1981). Foliage biomass at the stand level, reflected in measures such as leaf area, LAI, canopy cover, and mean crown completeness, is decreased. The crown width of remaining trees is increased compared to that of control stands, as a result of the increased survival of lower, longer branches. The rate of branch elongation is affected little by thinning, and so does not contribute to the increased crown width. Maximum foliage biomass is located lower in the crown, and thus a thinned stand has fewer trees, longer, wider crowns, and a lower peak in foliage biomass than an unthinned stand.

Effects of thinning on stand microclimate

Variations in the vertical distribution of biomass result in differences in stand microclimate. Thinning a conifer stand increases light intensity below the canopy at a rate proportionately greater than the rate of removal of trees or basal area (Bunnell *et al.* 1986). For example, removal of 12% of basal area in a balsam fir stand increased below-canopy radiation by 25% (Vézina 1965). The effect of a unit reduction in crown closure on below-canopy radiation is greater at lower than at higher crown closures (Figure 2). Presumably, that occurs because lower crown closures have less overlap, and removal of one unit of cover is more likely to result in an unimpeded path for light (Bunnell *et al.* 1986).

Thinning also increases throughfall precipitation, although the increases are much lower than the percentage reduction in basal area (Bunnell *et al.* 1986). Temperature regimes in thinned stands are expected to be intermediate between open areas and uncut forests. Data cited by Thomas (1979:113) show that maximum summer temperatures below partially cut mixed forests in northeast Oregon were slightly higher than those in clearcuts. Increased solar radiation and temperatures are expected to result in lower summer humidity in canopies of thinned than unthinned stands. Reduced transpiration resulting from reduced foliar biomass may also lower stand humidity (Brix and Mitchell 1986).

As stand openness increases, light and precipitation penetrate further into the canopy. If the site microclimate is suitable for lichen development, then increasing stand openness should result in a larger portion of the canopy providing suitable habitat for *Alectoria* and *Bryoria*. At some point, however, summer temperatures may become too high or humidity levels too low for optimum lichen development.

Duration of thinning effects

The increase in stand openness brought about by thinning is diminished by subsequent growth of crowns. Initial retardation of growth — known as shock effect — is sometimes observed. Thinning later increases height growth above that of controls (Brix 1981; Barclay and Brix 1985). The duration of the increase in stand openness brought about by thinning depends on the intensity of the treatment. In one study, removal of 17–24% of basal area increased below-canopy illumination 2.9–4.6 times immediately after thinning, but the effect was largely lost 7 years later (Savina 1956, cited in Bunnell *et al.* 1986). In another study, 7 years after the removal of two-thirds of the basal area in a Douglas-fir stand, both canopy cover and LAI were still significantly lower in the treatment stand (59% and 3.04, respectively) (Brix 1981). Another study found that 28 years after thinning, Douglas-fir plots spaced to 130–150 stems per hectare at age 25 still had leaf areas much lower than the control plot, whereas results at higher stocking levels were mixed (Binkley and Reid 1984).

Effects of chainsaw thinning on litterfall rates

Although thinning is expected to improve conditions for production of arboreal forage lichens on suitable sites, it may actually reduce availability of lichens to deer by reducing stand litterfall rates (Stevenson 1986). Thinning of a closed-canopy forest results in a decrease in litter production which is roughly proportional to the degree of thinning (Bray and Gorham 1964). Reukema (1964) showed that over a 13-year period, litterfall was nearly proportional to basal area in a set of Douglas-fir stands repeatedly thinned to various prescriptions. Woon (1970) found that spacing of 12-year-old Douglas-fir stands to prescriptions of 3.7 x 3.7 m or more greatly reduced litterfall rates. Gessel and Turner (1976) showed that thinning dramatically reduced total litter production in Douglas-fir stands of various ages in Washington.

There is ample evidence that thinning decreases total litterfall production, but it is unclear how long the effects endure. Thinning results in structural changes to a stand beyond mere reduction in number of trees. It decreases the proportion of biomass allotted to wood, bark and dead branches and increases the proportions in foliage and live branches (Barclay *et al.* 1986). It also reduces mortality (Barclay and Brix 1985). Thirty-six years after thinning, a *Pinus contorta* stand produced similar total litterfall, but markedly smaller amounts of branch litterfall than unthinned stands (Moir 1972). Those observations suggest that effects of thinning on the rate of woody litterfall, if not total litterfall, may be lengthy.

Effects of girdling on litterfall rates

The preceding comments apply to the type of thinning most commonly done in coniferous stands on Vancouver Island, in which unwanted trees are felled with chainsaws. Alternatively, however, trees may be killed by girdling, or by having herbicides such as monosodium methanearsenate (MSMA) or glyphosate introduced directly into the inner bark. Because the effects of herbicides on the lichens growing on treated trees, and on the ungulates that consume the lichens, are unknown, chemical thinning should not be used for winter range creation without further study (see Part 2).

The effects of thinning by girdling on stand microclimate and the structure of living trees are similar to those of chainsaw thinning. However, girdling results in a number of standing dead trees which may act as a substrate for lichens and a source of litterfall for some time. Retention of branches by snags created in this way has not been studied, but Cline *et al.* (1980) reported that naturally dying Douglas-firs 9–18 cm in DBH lost their limbs over a period of about 8 years following death, whereas snags 19–47 cm DBH lost their limbs over a 13-year period. Branch retention may be somewhat greater on xeric winter range sites because snags deteriorate more slowly on dry than on moist sites (Franklin 1986; J.P. Kimmins, pers. comm., 1986). If the trees are killed chemically, their deterioration rates may be affected by the herbicide and the mode of application (see Part 2).

THINNING METHODS AND MANAGEMENT TRADEOFFS

Management to produce arboreal lichens in the canopy is expected to require frequent thinnings and a final stand density lower than that optimal for silvicultural purposes. Such a management regime will result in reduced volume on an area basis, but increased growth and size of individual trees (Long 1985). Management for lichen production is compatible with browse production, but will not maximize snow interception (Nyberg *et al.* 1986).

The most promising approach to enhancing lichen production without drastically reducing litterfall rates is to thin the stand without falling trees. Girdling is expected to be most effective in maintaining litterfall when applied to trees larger than about 19 cm DBH, because the trees remain standing longer. In some cases, thinning by girdling will compete with commercial thinning, which may be economically viable in stands having 200 m^3/ha or more of merchantable volume in stems over 20 cm DBH (B. Nyberg, pers. comm., 1987). An advantage of non-falling methods over chainsaw thinning is that woody debris is produced over a period of years rather than all at once, resulting in a lower fire hazard (J. Harwijne, pers. comm., 1986) and less interference with wildlife movement.

If girdling is not used, then careful selection of treatment sites, spacing prescriptions and timing can help offset reductions in litterfall rates. Stevenson (1986) offered several recommendations for incorporating chainsaw thinning into a strategy for lichen enhancement. Lichen enhancement was recommended for stands in which a substantial dead crown region was present below the live crown, because dead branches on trees remaining after thinning would become a substrate for lichen development and a source of litterfall.

That recommendation, however, is incompatible with other considerations for winter range creation, which suggest thinning should begin around the time of crown closure (Nyberg *et al.* 1986). Later initiation of winter range creation is a possibility, but poses several other potential problems: excessive slash accumulation, low initial abundance of rooted forage plants, slower response of trees to release from competition, and difficulties with lichen inoculation from the ground.

Stevenson (1986) also recommended that xeric Douglas-fir sites be selected for lichen enhancement, because existing dead branches would be retained for the longest possible time. That recommendation is compatible with other winter range creation objectives, but is irrelevant if no dead crown region is present. Selective high thinning might not reduce amounts of woody litterfall as much as low thinning, but would represent a loss in forestry values for uncertain gain. Finally, she recommended that insofar as possible, dead and dying trees should be retained during thinning operations. Snag retention would not affect winter range creation or forestry values, but could be a safety hazard for workers.

Because of the many tradeoffs associated with the recommendations for lichen enhancement using chainsaw thinning, girdling appears to be a more attractive option. Incorporating girdling or chemical thinning into a management plan for winter range creation is discussed more fully in Section 3.

2.3.4 Lichen Inoculation

Techniques for inoculating young stands with lichen fragments, either through ground or aerial application, are being developed (Palmer 1986, 1987a, 1987b). Use of these techniques addresses the problem of inadequate natural dispersal into young stands (Stevenson 1988). The role of lichen inoculation in an overall strategy for lichen enhancement is discussed further in Section 3. Research and development of techniques for lichen inoculation are discussed in Part 2.

2.3.5 Fertilization

Fertilization, like thinning, increases diameter, height, and volume growth of individual trees (Barclay and Brix 1985). Fertilization, however, affects canopy structure differently than does thinning (Brix 1981). It increases the rate of branch growth, especially high in the crown, and increases the leaf area index, largely because of increases in needle size, number of needles per shoot, and number of shoots produced. Unlike thinning, which increases the amount of foliage in the lower portion of the crown,

fertilization increases the amount of foliage in the top half of the crown. It can thus be expected to decrease stand openness and therefore penetration of light and precipitation into the canopy. Those effects on stand microclimate, coupled with observations that rapidly growing twigs are a poor substrate for lichen attachment, indicate that fertilization reduces the ability of a stand to support arboreal lichens.

Fertilization is desirable in intensively managed forests because it increases growth and yield. Beneficial effects of thinning on stand productivity are best realized when thinning is combined with fertilization. Fertilization is largely compatible with other aspects of winter range creation, but it is not essential to realization of winter range values (Nyberg *et al.* 1986).

2.3.6 Pruning

Pruning, the removal of lower branches of the crown, results in loss of substrate for lichens and loss of a source of litterfall when branches die naturally. Pruning a few bottom whorls to encourage understory development would not likely affect lichen availability greatly. However, pruning to 5.5 or 11 m above the ground, as suggested by Nyberg *et al.* (1986), could significantly reduce the potential of a stand to support lichens. Those degrees of pruning are wholly incompatible with early inoculation, because most inoculated branches would be removed. Moderate pruning might be compatible with late inoculation or with natural colonization.

3 MANAGEMENT SCENARIOS

In this section we describe several possible management scenarios for enhancing lichen production. We evaluate how effectively each scenario improves conditions for lichen development and litterfall production, and identify tradeoffs with other winter range values and timber values.

We used the stand development model TASS (Mitchell 1975, 1980) to identify the effects of each set of management actions on key stand features. The features (described in Section 2.2.1) include canopy cover (CC), percent live crown (CLP), stand density index (SDI), annual height growth (AHG), basal area (BA), basal area of hard snags (SNBA), and snags per hectare (SNAGS). To convey additional information about the structure and timber value of the stands modelled, we have also included number of living trees per hectare (TREES), mean tree height (HT), and merchantable volume (MVOL). More explicit definitions of the variables are given in Appendix 1. Each scenario begins at age 10 with 4400 stems per hectare of Douglas-fir, and runs for 120 years. By age 130, most fluctuations in stand measurements have stabilized.

TASS was developed for Site Index 35, and its performance at other site indices has not been fully evaluated (J. Goudie, pers. comm., 1987). Site index, a measure of the capability of a site to grow trees, is the average height (m) of the 100 trees per hectare of largest diameter at breast-height age 50 (Mitchell and Cameron 1985). Site indices of areas considered for winter range creation fall between 27 and 42 for the Coastal Douglas-fir zone and 25 and 39 for the Coastal Western Hemlock zone. Because of suspected relations between lichen development and growth rate of trees (Section 2.2.1), optimum sites for lichen enhancement are likely on the lower side of those ranges.

Our results show changes in forest measures over time for a hypothetical stand at Site Index 35. On less productive sites, the same changes would occur over a longer time period. The timing of most of those changes in stands with lower site indices may be approximated by substituting the corresponding ages shown in Table 2. However, values of three of the variables — annual height growth, snags per hectare, and snag basal area — would be affected by a change to lower site indices. Annual height growth would be proportionately lower on less productive sites. The rate of snag deterioration is not proportionate to site index; at lower site indices, the number of snags and their basal area would decrease to lower levels or remain longer at lower levels before the next influx of snags occurred. In some cases, that effect might be offset slightly by slower deterioration of snags on xeric sites (Section 2.2.1).

Management scenarios were planned so that the following comparisons could be made:

1. lichen inoculation late in stand history of unmanaged (Scenario 1) vs. previously thinned stands (Scenario 2). This comparison is discussed in Section 3.1.
2. thinning by girdling from above (Scenarios 1–3) vs. from below (Scenario 4). Thinning from above (high thinning) removes some of the larger trees in a stand and is generally used when thinned stems are to be used commercially. Thinning from below (low thinning) removes the smallest trees. This comparison is discussed in Section 3.2.
3. lichen inoculation early (Scenarios 3 and 4) vs. later in stand history (Scenarios 1 and 2). This comparison is discussed in Section 3.3.

The following considerations affected prescriptions for management scenarios:

- The final density of 100 stems per hectare was that suggested by Nyberg *et al.* (1986) for areas of browse production.
- For optimum lichen production and rooted forage production (Nyberg *et al.* 1986), the canopy should not be allowed to close while the stand is to function as winter range. The time required for a stand to close after thinning increases with stand age.
- Trees to be thinned by girdling should be at least 19 cm DBH to remain useful as a substrate for lichens for about 13 years (Section 2.3.3).
- The time required for inoculated stands to achieve enough lichen abundance to provide forage is unknown. We assumed a 13- or 14-year period (at Site Index 35) between inoculation and the first thinning by girdling; that would correspond to a 17-year period at Site Index 30 and a 22- or 26-year period at Site Index 25.

TABLE 2. Ages at which corresponding heights are reached at Site Indices 25, 30 and 35 (Mitchell and Cameron 1985)

Height (m)	Site Index		
	25	30	35
3	12	11	10
6	17	15	14
9	22	19	18
12	27	23	21
15	33	27	25
18	39	32	28
21	47	38	33
24	56	43	37
27	66	50	42
30	79	58	47
33	95	67	54
36	116	78	60
39	143	90	68
42	180	106	77
45	233	125	88
48		149	100
51		180	114
54		222	131
57			151

Prescriptions for the management scenarios are given in Table 3. Effects of Scenarios 1–4 on key stand features are shown in Figures 4–7, respectively. Final values (at age 130) of selected stand measures are given in Table 4.

TABLE 3. Prescriptions for management scenarios

Scenario 1:	– chainsaw thinning from below to 500 stems/ha at age 28 – lichen inoculation immediately after thinning – thinning from above by girdling to 300 stems/ha at age 41 – thinning from above by girdling to 100 stems/ha at age 53
Scenario 2:	– chainsaw thinning from below to 700 stems/ha at age 14 – chainsaw thinning from below to 500 stems/ha at age 28 – lichen inoculation immediately after thinning – thinning from above by girdling to 300 stems/ha at age 41 – thinning from above by girdling to 100 stems/ha at age 53
Scenario 3:	– chainsaw thinning from below to 700 stems/ha at age 14 – lichen inoculation immediately after thinning – chainsaw thinning from below to 600 stems/ha at age 20 – thinning from above by girdling to 500 stems/ha at age 28 – thinning from above by girdling to 300 stems/ha at age 41 – thinning from above by girdling to 100 stems/ha at age 53
Scenario 4:	– chainsaw thinning from below to 700 stems/ha at age 14 – lichen inoculation immediately after thinning – chainsaw thinning from below to 600 stems/ha at age 20 – thinning from below by girdling to 500 stems/ha at age 28 – thinning from below by girdling to 300 stems/ha at age 41 – thinning from below by girdling to 100 stems/ha at age 53

TABLE 4. Stand measures at age 130 for each management scenario

	Scenario				
	0	1	2	3	4
TREES	394	62	77	77	101
BA	79.6	18.4	23.7	23.4	34.9
SDI	1221	262	333	330	482
HT	51.9	47.8	47.3	48.9	56.1
DBHQ	50.7	61.6	62.4	62.1	66.4
MVOL	1365	273	346	352	571

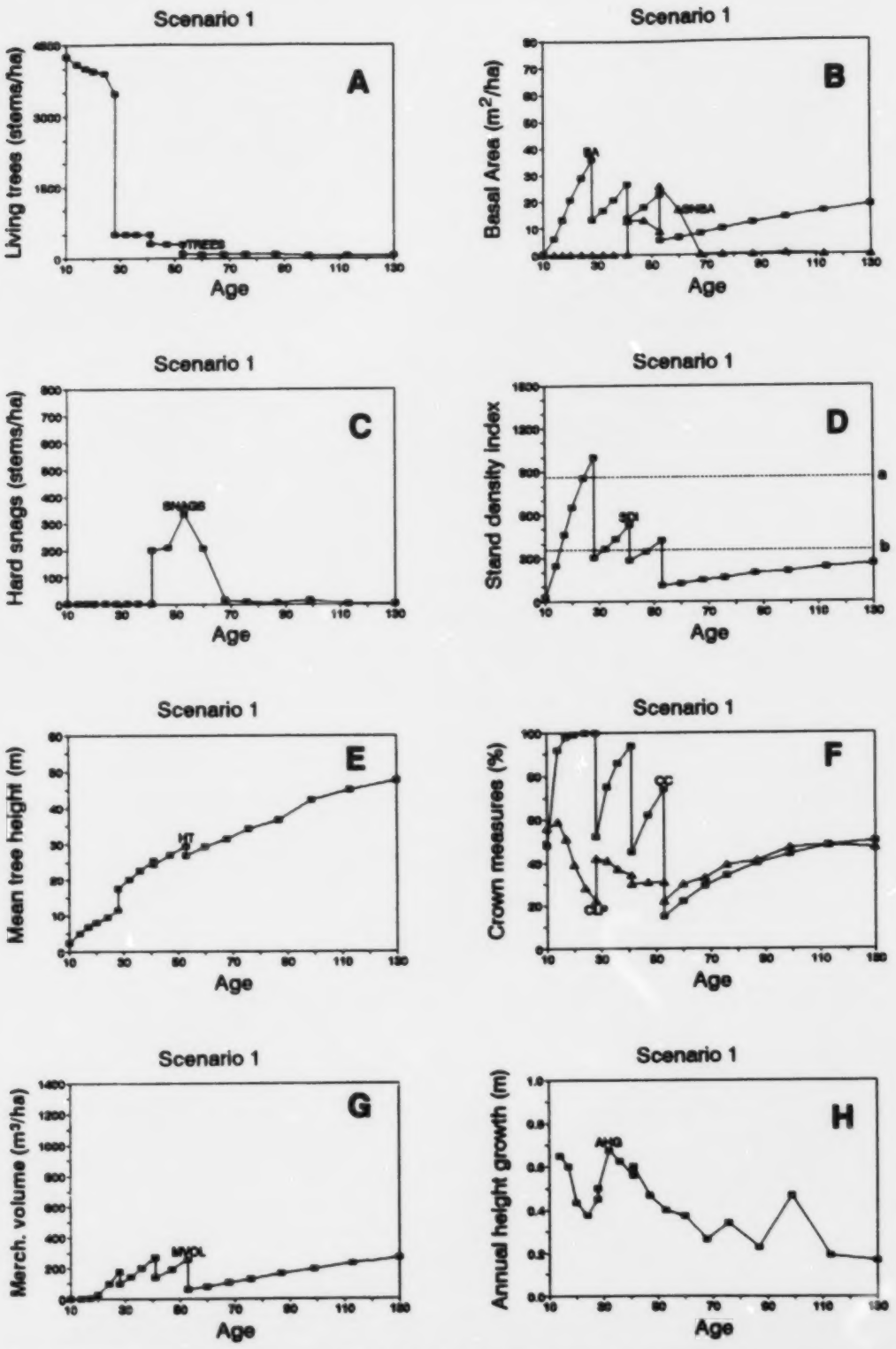

FIGURE 4. Scenario 1. A) TREES (stems/ha). B) BA and SNBA (m^2/ha). C) SNAGS (stems/ha). D) SDI: a = lower limit of self-thinning, b = onset of competition. E) HT (m). F) CC and CLP (%). G) MVOL (m^3/ha). H) AHG (m).

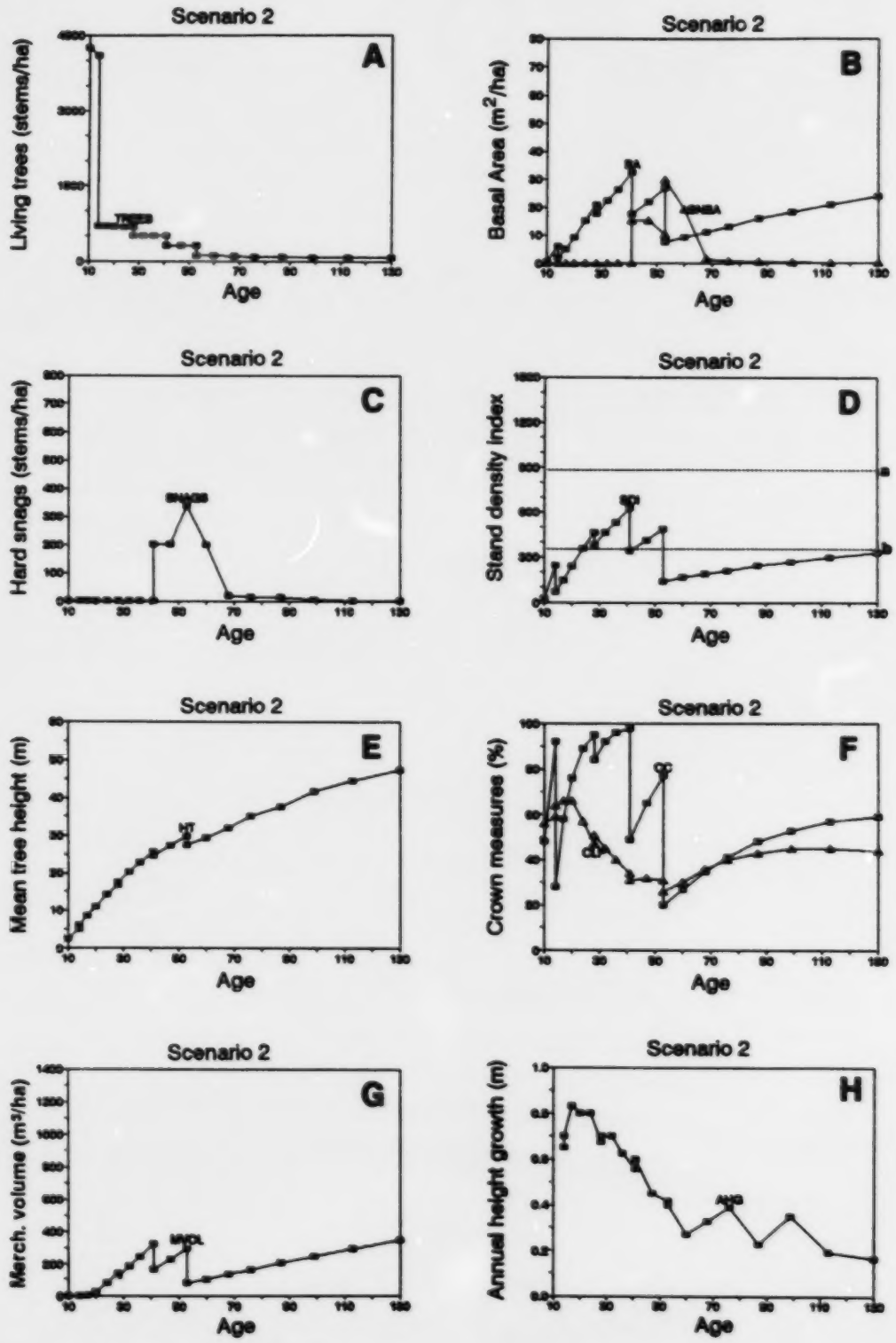

FIGURE 5. Scenario 2. A) TREES (stems/ha). B) BA and SNBA (m²/ha). C) SNAGS (stems/ha). D) SDI: a = lower limit of self-thinning, b = onset of competition. E) HT (m). F) CC and CLP (%). G) MVOL (m³/ha). H) AHG (m).

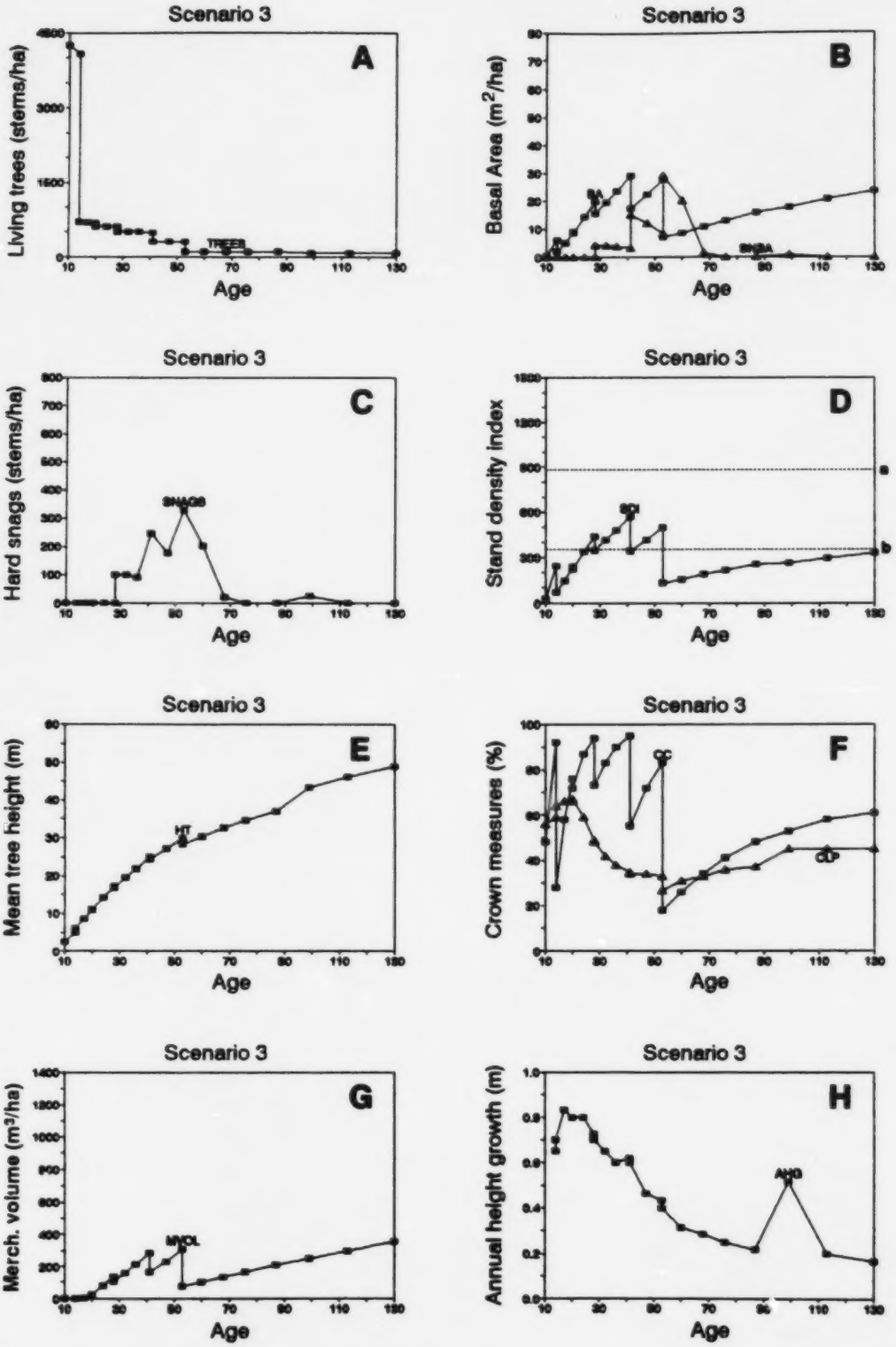

FIGURE 6. Scenario 3. A) TREES (stems/ha). B) BA and SNBA (m²/ha). C) SNAGS (stems/ha). D) SDI: a = lower limit of self thinning, b = onset of competition. E) HT (m). F) CC and CLP (%). G) MVOL (m³/ha). H) AHG (m).

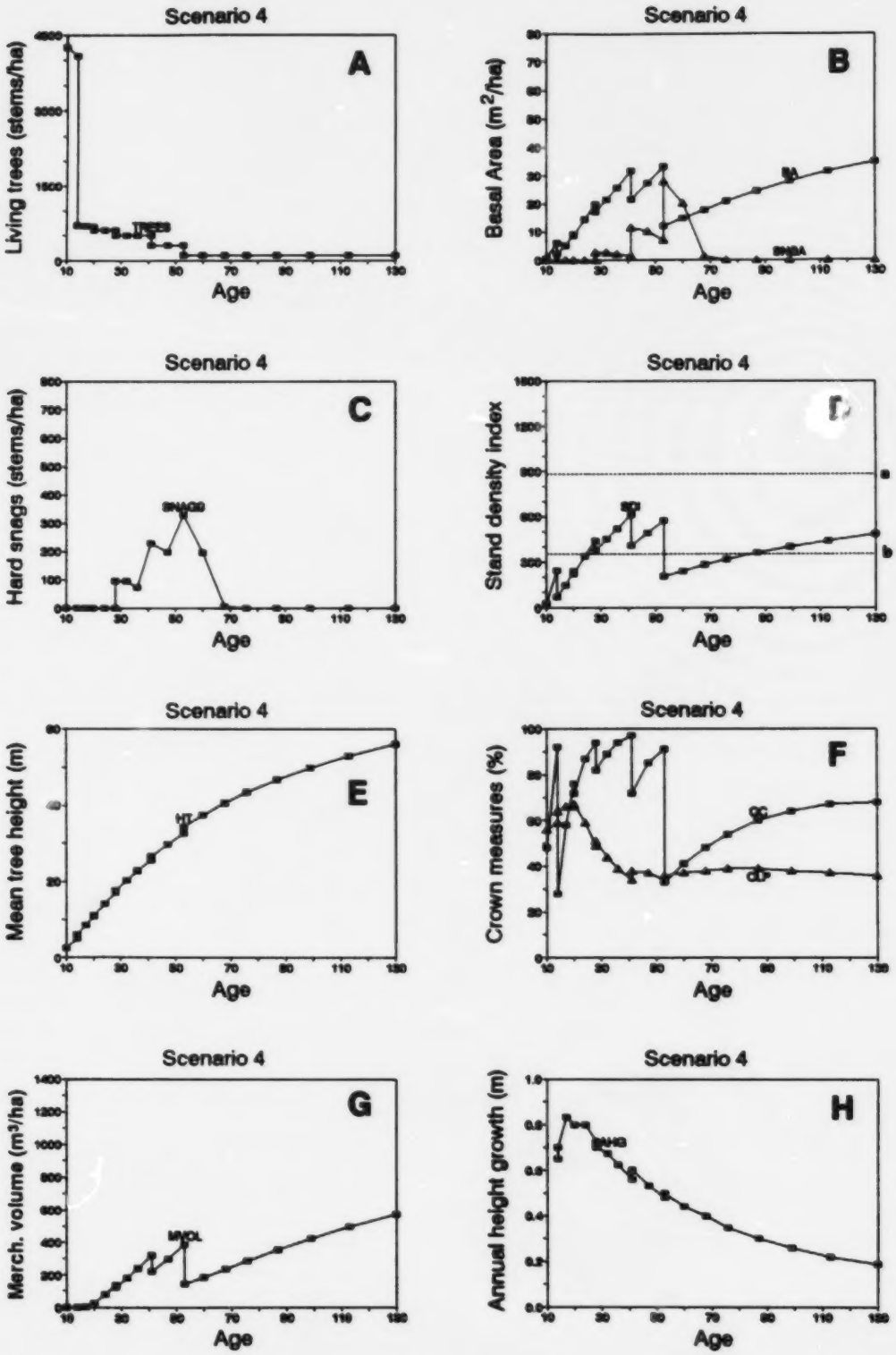

FIGURE 7. Scenario 4. A) TREES (stems/ha). B) BA and SNBA (m^2/ha). C) SNAGS (stems/ha). D) SDI: a = lower limit of self-thinning, b = onset of competition. E) HT (m). F) CC and CLP (%). G) MVOL (m^3/ha). H) AHG (m).

3.1 Scenarios 1 and 2: Inoculation of Unmanaged vs. Previously Thinned Stands

In parts of Vancouver Island, untreated stands that have already begun self-thinning are common. In this set of scenarios, we compare the effects of initiating winter range management at age 28 in unmanaged and previously thinned stands.

By age 28, the unmanaged stand has reached the young seral stage. The canopy has been fully closed for about 10 years, the stand density index has risen above the level of self-thinning, and the number of stems per hectare has begun to drop rapidly. Dieback of lower branches due to reduced light in the lower canopy is reflected in the decline of percent live crown.

The thinning that takes place at age 28 has dramatically different effects on stand openness in the two scenarios, even though the spacing prescription is the same. In the previously thinned stand, reduction in canopy cover and stand density index is slight, and recovery to previous values is rapid. In contrast, both measures drop significantly after thinning in Scenario 1, and are still below previous values by the time of the next thinning. In Scenario 2, the stand is probably too closed for either optimum lichen or browse production by 3–4 years after the thinning at age 28. Forage production could probably be improved if the first thinning were lighter and the second heavier.

Initial patterns of tree growth are markedly different in the two stands. As in the unmanaged stand (Section 2.2.2), average height growth rate is initially low in Scenario 1 because of the large number of suppressed trees, but is increasing at the time of inoculation. Mean tree height at the time of inoculation is the same, 17.4 m, in both scenarios. That occurs because height growth of dominant trees is affected little, if at all, by competition, and the other trees have been removed. There is, however, a possibility that on poorer sites, competition might adversely affect height growth of dominants, so that the height of the stand would be lower at the time of inoculation in Scenario 1 than in Scenario 2 (J. Goudie, pers. comm., 1987). Removal of suppressed trees during the first thinning in Scenario 1 brings percent live crown close to where it is in Scenario 2, and they remain at similar levels after that.

In Scenarios 1 and 2, woody litterfall from snags is maximized for a 27-year period that begins 13 years after inoculation. The number of snags produced is similar for both scenarios, but snag basal area is somewhat higher in Scenario 2 because of the snags' larger size.

Other deer winter range values are likely to differ in the two scenarios. When the first thinning occurs in Scenario 1, the canopy has been closed long enough that understory forage production has probably been reduced. Effectiveness of thinning treatments in bringing about recovery of the understory, once it has been reduced by crown closure, is questionable (Alaback 1984). Scenario 2, in contrast, is expected to maintain understory forage production if the thinning at 28 years is intensified. Scenario 2 has the additional advantage of reducing the number of stems early enough in stand history to minimize slash accumulation. In Scenario 1, slash levels after the first thinning could be great enough to impede animal movement. Snow interception would be sub-optimum in both scenarios, but that is expected of any management regime in which forage production is the primary objective.

The cost to timber values of delaying the initial thinning is reflected primarily in reduced merchantable volume (Table 4). Higher levels of slash accumulation expected in Scenario 1 would also be of concern to foresters, because of fire hazard.

In summary, early thinning followed by late inoculation (Scenario 2) is superior to late initiation of management (Scenario 1), if all resource values are considered. However, it would be necessary to alter the prescription so that the second thinning was more effective in reducing canopy cover. For a stand that has already reached the young seral stage without thinning, management for lichen enhancement is feasible, but its overall value as a winter range might be limited by reduced understory production and excessive slash accumulation.

3.2 Scenarios 3 and 4: Thinning from Above vs. Thinning from Below

In Scenarios 3 and 4, inoculation with lichens takes place at the earliest possible time in stand development, immediately after a thinning at 14 years. A second lighter chainsaw thinning is scheduled for age 20 to maintain canopy openness until lichens have grown enough that girdling will result in lichen litterfall.

In Scenarios 3 and 4 we test the effects of thinning from above and from below on the production of lichen standing crop and litterfall, on other winter range values, and on timber values. All thinnings from age 28 on in these scenarios are by girdling, intended to produce snags that will become a substrate for lichens and a source of lichen-bearing litterfall. Thus, the commercial value of thinned stems is lost. Thinning from above is a possible strategy for lichen enhancement because it results in larger snags.

Some adjustments in timing and intensity of thinning prescriptions would be necessary to maintain desirable levels of stand openness in both scenarios. The thinning at age 20, intended to maintain light penetration into the stand for both browse and lichen production, has little effect on canopy cover; that could be remedied if the first thinning were lighter and the second heavier. Thinning from below is less effective than thinning from above in reducing canopy cover. In Scenario 3, canopy cover drops to a lower level and does not return to as high a level as in Scenario 4. At age 53, canopy cover is only 20%, which may be too low for optimum lichen production on some sites. Stand density index remains below the onset of competition after the first spacing in Scenario 3, but not in Scenario 4. In Scenario 4, final canopy cover (68%) is somewhat higher than recommended for browse production by Nyberg *et al.* (1986).

After the series of thinnings from above has begun, annual height growth is somewhat lower in Scenario 3 than in Scenario 4, except for an apparent peak at age 99 (Section 2.2.2). It is unclear to what extent, if any, a difference in stand growth rate of that degree and at that time would affect lichen development. In both scenarios, inoculation takes place just before the peak in annual height growth. If rapid growth rates of the trees have a critical effect on the ability of lichen fragments to establish themselves, then age 14 may not be the best time to inoculate.

Mean tree height is 6.0 m at the time of inoculation, compared to 17.4 m in Scenarios 1 and 2.

In both scenarios, woody litterfall produced by snags is maximized for 40 years, beginning 14 years after inoculation. The differences between the two scenarios in the number and basal area of snags are not great. At age 28, there are slightly fewer snags in Scenario 4 because a few of the thinned stems are too small to be included in calculations. Their basal area is much lower (62% of that in Scenario 3) because smaller trees are being taken from an otherwise identical stand. The mean diameter of snags created is 23.0 cm in Scenario 3 and 17.8 cm in Scenario 4.

At age 41, the number of snags is slightly lower in Scenario 4 because there are no natural mortalities, all suppressed trees having been thinned. The mean diameter of the new snags (24.8 cm) has increased in relation to that of Scenario 3 (28.8 cm). The lower number of snags and lower mean diameter together keep their basal area to 77% of that of Scenario 3.

At age 53, the number of snags in the two scenarios is the same. The trees have grown enough in Scenario 4 that the mean diameter of new snags created by thinning from below (35.8 cm) is identical to the mean diameter of new snags created by thinning from above in Scenario 3. Snag basal area is very slightly lower in Scenario 4 because the snags remaining from the previous thinning are smaller than in Scenario 3.

After age 68, slightly more snags are produced in Scenario 3 than Scenario 4 because there is some continuing mortality of suppressed trees.

These results indicate that increases in size and longevity of snags gained by a program of thinning from above rather than below are not great, and decrease with time. Advantages of thinning from above are offset by the smaller average DBH of the stand. A better strategy for enhancing lichen litterfall might be to thin selectively, including a small number of larger trees (especially those low in timber value and/or supporting above-average lichen loads), along with suppressed trees. Those prescriptions would be most appropriate for the first two girdling treatments, and would probably be unnecessary by the time of the third thinning.

The winter range values of the two scenarios are not markedly different. As described above, minor adjustments in thinning prescriptions could be made to optimize canopy cover for browse production. Differences in mean tree height and percent live crown between the two scenarios might affect snow interception, but that is a secondary criterion for forage production areas.

A stand thinned from above has much lower value to the forest industry at time of harvest than one thinned from below. Mean tree height, quadratic mean diameter (DBHQ), and merchantable volume are all markedly lower at the end of Scenario 3 than at the end of Scenario 4 (Table 3). Those differences could be reduced somewhat by adjusting the thinning prescriptions so that the final number of trees was the same in the two scenarios.

In summary, it appears that the advantages of thinning from above to increase lichen litterfall production are not great, and are outweighed by a high cost to the forest industry. We recommend instead that a prescription of selective girdling, in which a small number of larger trees are included with the suppressed trees, be applied when it is necessary to boost litterfall production.

3.3 Scenarios 1–2 and 3–4: Late vs. Early Inoculation

Simulations cannot provide a final answer to the question of early vs. late inoculation, but they can help us focus on the critical factors that will affect results, and thus can help us guide research. Early inoculation, as in Scenarios 3 and 4, allows the longest possible time for lichens to grow. Inoculation takes place when the trees are short (6 m, in the scenarios tested) and growing rapidly. Short trees are easier to inoculate from the ground than larger trees. However, the part of the tree that is inoculated later becomes the lower portion of the crown. It is uncertain whether that location will be suitable over the long term for rapid lichen growth. It is also uncertain to what extent lichens will extend their distribution higher into the crown.

In the late inoculation scenarios, trees are much taller (17.4 m) and their height growth rate has begun to decline. Thus, larger crowns are present to be inoculated, and inoculated portions of the crowns are overtopped more slowly. Empirical research will be required to test the relative importance of those factors in determining the long-term success of lichen inoculation.

3.4 Discussion

One of the benefits of using a computer model such as TASS to simulate effects of management is that unnecessary treatments can be eliminated without field trials (Mitchell 1975). In this case, thinning by girdling from above rather than below was projected to have little value in increasing woody litterfall, the objective for which the treatment was suggested. Use of models for novel applications, such as predicting suitability of a stand for growing lichens, has limitations which must be recognized. Results depend on our imperfect understanding of relations between stand features that are modelled (or can be derived from the model) and variables of interest, such as production of lichens, litterfall, or browse. Also, models have been tested empirically with data from a limited range of sites. In this case, very wide spacing of trees and low site indices were outside the range of data on which the model was based (J. Goudie, pers. comm., 1987).

In assessing impacts of management actions on suitability of a stand for producing lichens, we have relied heavily on stand openness, as reflected in canopy cover and stand density index. However, the optimum range of stand openness for lichen production is unknown. In the absence of specific information, we have assumed that if the canopy is open enough to encourage browse production on the forest floor, it is open enough to permit lichen production in the canopy. The optimum range of canopy closure for browse production is thought to be 30–60% (Nyberg *et al.* 1986). We suspect that canopy closures at the lower end of that range or below it would be suboptimum for lichen production on some sites.

All scenarios presented here would require some adjustment in thinning prescriptions to maintain crown closures in the 30–60% range as much of the time as possible. In general, canopy cover is well above 60% most of the time before the final thinning, but remains acceptably low after that. The thinnings at ages 20 and 28, particularly, should be intensified; the one at age 14 is heavier than necessary.

Some interpretations of the scenarios and assessments of the impact of management practices (Section 2.3) are based on the assumption that rapidly growing trees offer a poor environment for lichen development. That assumption should be investigated empirically, as it has important implications for compatibility of lichen enhancement and other management objectives.

The management scenarios described here incorporated girdling rather than chainsaw thinning to provide a steady input of woody litterfall as much as possible during the period that the stand functions as winter range. In Scenarios 1 and 2, woody litterfall from snags is maximized from ages 41 to 68, and in Scenarios 3 and 4 from ages 28 to 68. The period of litterfall production by snags could be lengthened by adjusting the timing and intensity of the thinnings. After the last artificially created snags have deteriorated, the ability of the stands to produce lichen litterfall is unknown. Final basal area in all thinned stands is much lower than that in the untreated stand (Table 3), suggesting that woody litterfall rates are also much lower. However, lichen standing crop may have reached such a high level by this time that litterfall of unattached lichens will provide adequate forage levels.

Because girdling is applied relatively late in stand history in these scenarios, stems that are treated may represent volume that could be harvested commercially. Commercial thinnings may be feasible once 200 m^3 or more of timber is available to be harvested in stems over 20 cm DBH (B. Nyberg, pers. comm., 1987). The third girdling treatment in Scenario 4, in which 241 m^3 of timber are treated, could be a commercial thinning if logging costs were low. In general, however, the requirement for an open canopy in forage production areas implies stem densities so low that commercial thinnings would be marginal.

4 SUMMARY

The best winter range conditions for black-tailed deer on Vancouver Island are typically found in old-growth stands. The demand to harvest old-growth timber has led managers and researchers to search for ways of managing second-growth stands so that they will meet the needs of deer for winter ranges.

The arboreal lichens *Alectoria sarmentosa* and *Bryoria* spp. are important winter foods for black-tailed deer, especially when other forage is covered by deep snow. Availability of those lichens to deer depends both on their abundance in the canopy, and the rate at which they fall to the forest floor. Typically, the standing crop and litterfall rates of arboreal lichens are high in some old-growth stands, but low in second growth.

Models for managing young stands to enhance cover and understory forage have been developed, but management activities necessary for lichen enhancement in those stands were not formulated. Our objectives in this report were:

1. to develop models for managing young stands to enhance lichen forage as well as other winter range values; and
2. to describe research that is needed to integrate lichen enhancement into a winter range creation program.

Objective 1 is addressed in Part 1 of this report; Objective 2 in Part 2.

For our model, we described conditions that are necessary for lichen colonization, growth and litterfall production to occur. We described the development of unmanaged stands in relation to the production of lichens and litterfall, and identified a set of key stand features that are indicative of a stand's potential to produce lichen forage. Finally, we described how those key stand features are affected by forestry practices.

Dispersal

For *Alectoria sarmentosa* and *Bryoria* spp. to become established in a young stand, lichen fragments must be transported into the stand and deposited on suitable substrate. Levels of dispersal of lichen fragments are very low except within 300–400 m of mature timber stands with above-average lichen abundance. Managers

have two options for ensuring that lichen propagules arrive in young stands that are to be managed as winter ranges. They can retain natural sources of lichen propagules — patches of old growth, veterans or snags that support abundant lichens. The quantity and spatial arrangement of residual timber necessary to enhance lichen dispersal is not known. Alternatively, young stands can be inoculated with fragmented lichens. A pilot study of inoculation has been conducted, and plans to develop the methodology are included in Part 2 of this report.

Substrate

The normal substrate for *Alectoria sarmentosa* and the arboreal *Bryoria* species is the bark of coniferous trees. Douglas-fir and western hemlock apparently offer better substrate conditions than do western redcedar. Lichen development may be limited by bark smoothness in the very young part of the crown. The smooth bark and widely separated needles of twigs that have grown rapidly are particularly unfavourable for lichen establishment.

Microclimate

Observations of the distribution of *Alectoria sarmentosa* and *Bryoria* spp. suggest that the optimum environment for those species is one of high radiation, high input of moisture, high evaporation rates, and, therefore, frequent cycles of wetting and drying. From the time canopy closure occurs until natural thinning increases penetration of light and precipitation into the canopy, the microclimate of most unmanaged second-growth stands is poorly suited to lichen development. Although conditions on the upper branches may support lichens, those branches are quickly overtopped and shaded. Fertilization increases branch growth rates, especially high in the crown, and is expected to hamper lichen growth. Increasing the openness of the stand by thinning is expected to benefit lichens by creating suitable habitat for lichens in larger areas of the canopy.

Some sites may be too warm or too dry for optimum lichen development. Because spacing of young stands will maintain warmer, drier canopy conditions for longer periods of time, it is important to identify the limits of tolerance of *Alectoria sarmentosa* and *Bryoria* spp. to low moisture and high temperature.

Time

Lichens need time to develop from small thallus fragments to clumps that are large enough to be useful as forage. The observation that lichens are occasionally abundant in immature stands indicates that they have the potential to grow fairly rapidly, although that potential is not usually realized. Direct and indirect estimates of annual growth rates of fruticose arboreal lichens have ranged from 5 to 29.4% annually. Growth projections suggest that the time required to achieve high levels of lichen biomass is sensitive to small differences in annual growth rates and in initial lichen biomass.

Litterfall

Rates of lichen litterfall are related to the standing crop of arboreal lichens and to the overall rate of litterfall in the stand. Litterfall rates are generally somewhat lower in young stands than in older stands, but are high enough to provide substantial amounts of forage if special management practices succeeded in enhancing the standing crop of the lichens. However, ordinary thinning practices reduce stand litterfall rates significantly.

Thus, thinning may increase arboreal lichen production without benefiting deer because so little of the lichen becomes available through litterfall.

In contrast, thinning by girdling results in a number of standing dead trees which are expected to act as a substrate for lichens and a source of litterfall for some time.

Management scenarios

The elements of management for lichen enhancement are chainsaw thinning early in stand history, inoculation with lichen fragments, and thinning by girdling later in stand history. The stands must be kept open to maximize the production of understory forage as well as lichens.

We used the stand development model TASS to identify the effects of several different management scenarios on a number of key stand features which are related to suitability for lichen production: canopy cover, percent live crown, stand density index, annual height growth, basal area, and basal area of snags. We evaluated how effectively each scenario would improve conditions for lichen development and litterfall production, and identified tradeoffs with other winter range values and timber values.

In parts of Vancouver Island, untreated stands that have already begun self-thinning are common. Our analysis indicates that management for lichen enhancement in such a stand is feasible, but that its overall value as a winter range might be limited by reduced understory production and excessive slash accumulation.

Thinning from above (removal of the larger rather than the smaller stems) has been suggested as a possible strategy for lichen enhancement because it results in larger snags if the trees are killed by girdling. Our analysis indicates that the increase in litterfall production gained from thinning from above would not be great, and would be outweighed by a high cost to the forest industry. We recommend instead that a prescription of selective girdling, in which a small number of larger trees are included with the suppressed trees, be applied when it is needed to boost litterfall production.

The best stage in stand development for lichen inoculation is not known. Early inoculation (age 14 in our scenarios) allows the longest possible time for lichens to grow. Trees are short (6 m) and growing rapidly at the time of inoculation. The portion of the tree that is inoculated later becomes the base of the crown. It is uncertain whether that location is suitable for rapid growth, and whether lichens will extend their distribution higher in the crown.

In the late (age 28) inoculation scenarios, trees are much taller (17.4 m) and their height growth has begun to decline. Thus, larger crowns are present to be inoculated, and the inoculated portions of the crowns are overtopped more slowly. Empirical research will be required to test the relative importance of those factors in determining the long-term success of lichen inoculation.

Because girdling is applied relatively late in stand development in the lichen enhancement scenarios, stems that are treated may represent volume that could be harvested commercially. Our analysis indicates that the need for an open canopy to produce rooted forage as well as lichens would mean stem densities so low that commercial thinnings would likely be marginal.

APPENDIX 1. Variables used in management scenarios

All variables used in management scenarios are based on the output variables of the stand development model TASS (Mitchell 1975, 1980) as defined below:

TREES – Living trees (stems/ha)

SNAGS – Hard snags (Stage 1 or 2 of Cline *et al.* 1980) ≥9 cm DBH. Snags 9–18, 19–47 and >47 cm DBH were assumed to remain in Stages 1–2 for 8, 13 and 18 years, respectively, and to follow survival curves I, II and III, respectively (Cline *et al.* 1980: Figure 4).

BA – Basal area (m^2/ha)

SNBA – Basal area of hard snags ≥9 cm DBH. The basal area of new mortalities for each time period was calculated from TASS gross production data:

SNBA (new mortalities) = (GROSS BA – STAND BA) $_{t2}$ – (GROSS BA – STAND BA) $_{t1}$

where $_{t2}$ is the end and $_{t1}$ is the beginning of the time period.

The diameter class of the new mortalities was determined in one of two ways:

1. In the case of mortalities resulting from chemical spacing, the BA in each diameter class was calculated from stand and stock tables.
2. In the case of natural mortalities, diameters could not be determined from standard stock tables. We assumed that most new mortalities originated from the suppressed classes, and used the 25th quartile of the DBH distribution from the previous age to approximate the average DBH of new snags entering the snag pool.

SNBA was assumed to diminish over time in the same manner as SNAGS.

SDI – Stand density index (Reineke 1933):

$SDI = TREES(DBHQ/25)^{1.6}$

DBHQ – Diameter at breast height of the tree of mean basal area

HT – Mean tree height (m)

MVOL – Merchantable volume (m^3/ha)

CC – Percent of the ground area covered by tree crowns

CLP – Length of live crown (from the second live whorl to the top) relative to tree height (%)

AHG – Annual height growth

APPENDIX 2. Personnel contacted

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